

The Family Position of Neotropical Frogs Currently Referred to the Genus *Pseudis*

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(Text-figures 1-5)

RECENTLY while reviewing the classification of several aquatic frog genera from South America we had an opportunity to consider the genus *Pseudis* in some detail. One member of this genus, *Pseudis paradoxus* of eastern South America, has long ranked with the African hairy frog, *Astylosternus robustus*, the casque-headed frogs of the Americas, the West African giant frog, *Rana goliath*, and the neotropical marsupial frogs, as a constant source of popular interest by reason of its change at metamorphosis from a giant tadpole to a relatively small adult. It is surprising that this herpetological curiosity and its close allies are not well understood systematically, for our investigations reveal that the genus is composite and that the status of the described species is badly confused. Moreover, it has been discovered that the reference of *Pseudis paradoxus* and related forms either to the family Leptodactylidae (sensu lato) or to the family Hylidae is questionable. The following notes are a result of our analysis of these problems and are designed to clarify the systematic position of these "paradoxical" frogs.

HISTORICAL ACCOUNT

In this summary of the history of the frogs allied to *Pseudis paradoxus*, only those papers are cited in which new genera or species are proposed or which contain radical changes in the placement of named forms. For complete synonymies see Berg (1896), Nieden (1923) and Miranda-Ribeiro (1926). Throughout this preliminary discussion specific names are presented as they appear in the papers under consideration. It should be noted, however, that both the generic names *Pseudis* and *Lysapsus*

are of masculine gender following the International Rules of Zoological Nomenclature as modified at the Paris Congress (see Hemming, 1950, p. 109).

Rana paradoxa was first described in the modern systematic literature by Linnaeus (1758, p. 212) from a series of transforming tadpoles now in the Royal Museum at Stockholm (Andersson, 1900, p. 21). Laurenti (1768, p. 35) included the larvae of this frog in his genus *Proteus* as a new species, *P. raninus*. During the next sixty years all other workers followed Linnaeus and it was soon recognized that Laurenti's name applied to larvae of *Rana paradoxa*.

Wagler (1830, p. 203) delineated the differences between *paradoxa* and the rest of Linnaeus's *Rana* and proposed the genus *Pseudis* for this unique frog. Duméril & Bibron (1841, p. 330) followed Wagler but changed the name to *Pseudis merianae*.

Günther (1858, p. 6) recognized a second species of the genus from a single specimen collected by Charles Darwin in South America. The new frog, *Pseudis minuta*, was distinguished from *P. paradoxa* because of its small size and longer legs.

Cope (1862a, p. 155) described a small aquatic frog from Uruguay as a new genus and species, *Lysapsus limellum*, which differed from *Pseudis paradoxa* in the presence of expanded disks on the fingers and in the placement of the prevomerine teeth behind the choanae (fingers simple and prevomerine teeth between choanae in *paradoxa* and *minuta*). It was not until later in the same year that Cope (1862a, p. 353) recognized the affinity of *Lysapsus* with *Pseudis*. This was occasioned by his description of *Lysapsus mantidactyla* from Buenos Aires, Argentina.

The major differences between *L. limellum* and *L. mantidactyla* were in size, the former being about the size of *P. minuta* and the latter approaching the length of *P. paradoxa*. Unfortunately Cope makes no mention of the condition of the tips of the fingers or the position of the prevomerine teeth in *mantidactyla*, an oversight which has caused considerable confusion. Adding to this confusion is the fact that he did not explicitly distinguish *Lysapsus* from *Pseudis*.

Steindachner (1864, p. 262) inadvertently proposed a new generic and specific name for Cope's *limellum* when he cited a manuscript name of Fitzinger's in the synonymy of *Pseudis minuta* (nec Günther). This generic name, *Podonectes*, is a strict synonym of *Lysapsus* and its montotype, *P. palmatus*, is the same as Cope's *L. limellum*.

Pizarro (1876, p. 34) used the name *Batrachichthys* for the larva of *Pseudis paradoxa* but listed no specific name.

Boulenger (1882, p. 186) placed *Lysapsus* in the synonymy of *Pseudis* and recognized *paradoxa*, *minuta*, *limellum* and *mantidactyla*. Misinterpreting Cope's reference of the last named form to the genus *Lysapsus* as meaning that it had disked fingers, he divided *Pseudis* into two parallel series each with a large and a small representative (*paradoxa-minuta* group and *mantidactyla-limellum* group).

Garman (1883, p. 47) distinguished a new form, *P. fusca*, collected in the Rio Arassuahy, Estado de Minas Geraes, Brazil, which he thought allied to *paradoxa* and *mantidactyla* because of its large size. The species differed from those forms in having only the tips of the toes dilated (both fingers and toes dilated in *mantidactyla*, neither fingers nor toes dilated in *paradoxa*, according to Boulenger).

Lutz (1925, p. 137) recognized a new species from Estado de Minas Geraes, Brazil, as *Pseudis bolbodactyla*. This frog was considered to be different from *paradoxa* because of the smaller size and dilated condition of the fingers and toes. Apparently Lutz's paper appeared too late for inclusion in Miranda-Ribeiro's publication cited next below.

Miranda-Ribeiro (1926, p. 27), in his basic work on the amphibians of Brazil, presented a review of the genus and the description of a new form, *Pseudis meridionalis*, from the Estado do Rio Grande do Sul. *Meridionalis* was supposed to be allied with *P. limellus* and differed from it only in the absence of disks on the fingers and toes.

Parker (1935, p. 510) described a new frog from British Guiana and Bolivia as *Pseudis laevis*. It was said to be related to *P. limellum*

but was differentiated from it because the skin was smooth instead of spinate.

No new species have been described since the publication of Parker's paper and no one has considered the relationships of the seven recognized forms.

STATUS OF THE GENUS LYSAPSUS

Pseudis as generally understood consists of two rather different types of frogs. These two stocks are markedly distinguished from each other in the structure of the digits, the relationships of the skull bones and the condition of the pectoral girdle. The differences in these features between *Pseudis paradoxa* and *Pseudis limellus* are of such magnitude and variety that generic segregation seems warranted. The species *paradoxa* is the type of the genus *Pseudis* and the first generic name available for *limellus* is *Lysapsus*.

The following information on the characteristics of these genera and their family position is derived from study of a large series of *limellus* and *paradoxa* from Brazil and a cleared and stained example of each species. Fortunately most of the features of importance in this group can be discerned without complete dissection.

GENUS PSEUDIS Wagler

Type of Genus.—*Rana paradoxa* Linnaeus, 1758, monotype.

Diagnostic Characters.—Fingers simple; toes somewhat expanded, webbed to middle of terminal dilations, which are small; terminal phalanges rounded, not claw-like. Maxillary and premaxillary teeth relatively long, pointed toward the center of mouth and in an oblique plane to roof of mouth; prevomerine teeth in two short series between the choanae; palatines strong, extending medially so that they lie behind the prevomerine tooth patches. Pectoral girdle with a partially ossified omosternum which is much shorter than the epicoracoid cartilages.

GENUS LYSAPSUS Cope

Type of Genus.—*Lysapsus limellum* Cope, 1862, monotype.

Diagnostic Characters.—Fingers and toes with well-developed disks; toes webbed to base of terminal expansions, which are relatively large; terminal phalanges pointed, claw-like. Maxillary and premaxillary teeth rather short, pointed downward towards floor of mouth at a vertical to roof of mouth; prevomerine tooth patches located far behind choanae; palatines weak, extending to a point lateral to prevomerine teeth and on a level with them. Pectoral girdle with

an entirely cartilagenous omosternum which is as long as epicoracoid cartilages.

In addition to the differences emphasized in the diagnostic characters, these genera differ in the general form of the skull (in *Pseudis* the snout is markedly curved anteriorly; in *Lysapsus* the snout is not as curved), the shape of the premaxillary and its anterior and posterior projections, the form of the prevomerine bones and their relationship to the choanae, the shape of the basal portion of the terminal phalanges, the size and shape of the penultimate phalanges, the shape of the omosternum and xiphisternum and the position of the right epicoracoid cartilage. These dissimilarities, except the cranial shape, are illustrated in Text-figs. 1, 2, 3 and 5. *Pseudis paradoxus* has been reported to occur in localities from eastern Venezuela south to Paraguay and Argentina. Our material is from São Luis de Cáceres, Estado de Matto Grosso, Brazil. *Lysapsus limellus* appears to have an extensive range in western and central Brazil south into northern Argentina. We have examples of *limellus* from the same locality as cited for *P. paradoxus*, Município Monte Alegre, Estado do Pará, Brazil, and the lower Madeira River in Estado do Amazonas, Brazil.

ALLOCATION OF DESCRIBED SPECIES

The generic position of the other recognized species of this group remains to be determined. They may be considered in the order of their description.

Günther's (1858) *minutus*, now known to occur in the Provinces of Entre-Rios, Corrientes and Misiones in Argentina, Uruguay and Estado do Paraná and Estado do Rio Grande do Sul in Brazil, may be placed in the genus *Pseudis* on the basis of the simple fingers, the complete webbing of the toes and the position of the prevomerine teeth between the choanae. This species appears to differ from *P. paradoxus* only in size and longer legs, although additional material may reveal other differences. We have seen no examples of *minutus*.

The description by Cope (1862a) of *Lysapsus mantidactylus* is far from adequate but various authors have assigned specimens from southern Brazil and Argentina to this form. While Cope makes no statement regarding the structure of the fingers in his species, Boulenger (1882), apparently misled by its reference to *Lysapsus*, concluded that both the fingers and toes were disked. In this assumption he has been followed by all subsequent workers including Miranda-Ribeiro (1926). The latter author, at the time of the publication of his work on the frogs of Brazil, had seen no specimens that he considered to be *mantidactylus*. Later he did obtain ex-

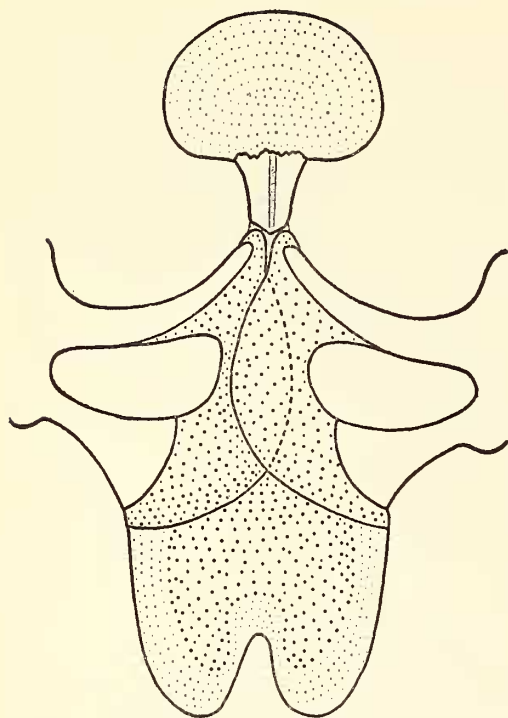
amples of the species and rewrote his description for the issuance of an unpublished second edition. A copy of this manuscript is in our possession and in it Miranda-Ribeiro points out the absence of disks on the fingers of *mantidactylus*. He also mentions that the tips of the toes in this form are dilated although not to the same extent as in *L. limellus*. This latter point was also made by Cope in the original description but Boulenger's assumption regarding diskings of fingers and toes has obscured this fact. All Brazilian material of large *Pseudis* seen by us fits Miranda-Ribeiro's revised description of *mantidactylus* and is almost certainly of Cope's species. It should be noted that all *Pseudis* and *Lysapsus* have the toes expanded at the tips. These expansions are most noticeable in *L. limellus* but are also present in *P. paradoxus*, although few descriptions mention them. In *Lysapsus* the finger tips are enlarged into disks. *Pseudis* is without disks although the finger tips may be slightly swollen (see Text-fig. 5). The swelling of the terminal portion of the fingers in *P. paradoxus* have been referred to in the literature as an expansion or dilation. Various authors have interpreted this to mean that *Pseudis* possess disks on the fingers. This is not true. Apparently all *Pseudis* have simple pointed fingers without terminal disks.

While no material of *P. paradoxus* from northern South America has been examined, no differences mentioned in the literature would separate northern *paradoxus* from Brazilian examples. Under the circumstances it seems best to regard *mantidactylus* as identical with *P. paradoxus*. The reference by Müller & Hellmich (1936, p. 27) of Argentine *Pseudis* to *paradoxus* supports this view.

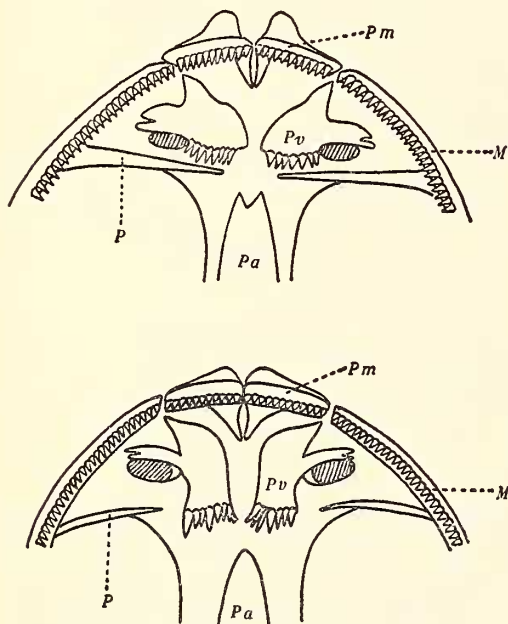
Garman's (1883) description of *Pseudis fuscus* is apparently based upon Minas Geraes examples of *paradoxus*. He also refers to the dilation of the toes and Miranda-Ribeiro (1926) interpreted this as meaning that they were disked as in *limellus* and different from *P. paradoxus*. As explained above, *paradoxus* has the tips of the toes slightly dilated.

Pseudis bolbodactylus Lutz, 1925, is based upon material from the same general region as the type of Garman's *P. fuscus*. Its description differs in no way from that of typical Brazilian *paradoxus* and may be referred to the synonymy of that species.

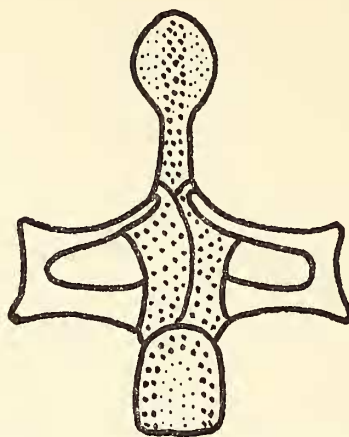
Pseudis meridionalis Miranda-Ribeiro, 1926, was originally differentiated from *L. limellus* because of the simple fingers. This form is distinguished from *P. minutus* by the presence of spinous warts on the back and legs. The type locality of *meridionalis*, from the Estado do Rio



TEXT-FIG. 1. The pectoral girdle of *Pseudis paradoxus* (Linnaeus).



TEXT-FIG. 2. Cranial elements of the roof of the mouth in *Pseudis paradoxus* (upper) and *Lysapsus limellus* (lower). Diagrammatic. Symbols represent the following bones: M, maxillary; P, palatine; Pa, parasphenoid; Pm, premaxillary; Pv, prevomer.



TEXT-FIG. 3. The pectoral girdle of *Lysapsus limellus* Cope.

Grande do Sul, Brazil, is within the known range of *minutus*, examples of which were not seen by Miranda-Ribeiro at the time he described *meridionalis*. We suspect his species to be a synonym of *minutus* but until the type of *meridionalis* is examined the species is given tentative recognition.

Pseudis laevis Parker, 1935, was described from material from the Rupununi Savanna, British Guiana, and one specimen from the Rio Beni, Bolivia. This form seems almost identical with *limellus* except in having smooth skin instead of the skin on the back being covered with spines. In his discussion of the ranges of these forms Parker states that *limellus* is restricted to the Paraguay-La Plata river systems of southern South America. He later modifies (1939, p. 87) this statement, suggesting an Amazon Basin distribution for the species. We have seen no smooth-skinned frogs of the *limellus* type although we have material of *limellus* (taken in Municipio de Monte Alegre, Estado do Pará, Brazil) from near the type locality of *laevis*, and Müller & Hellmich (1936, p. 26) have reported it from the Ilha de Marajó in the mouth of the Amazon. We also have examples of spinate *Lysapsus* from the Rio Madeira, Estado do Amazonas, Brazil, the same river into which drains the Rio Beni, the second locality for *laevis*. These records and the wide gap (Bolivia to British Guiana) between *laevis* localities suggest that the latter species might be based upon non-spinate *limellus*. The disked fingers and the position of the vomerine teeth leave little doubt as to the generic placement of Parker's specimens. Until thorough examination of critical material is made, we tentatively recognize *laevis* as valid.

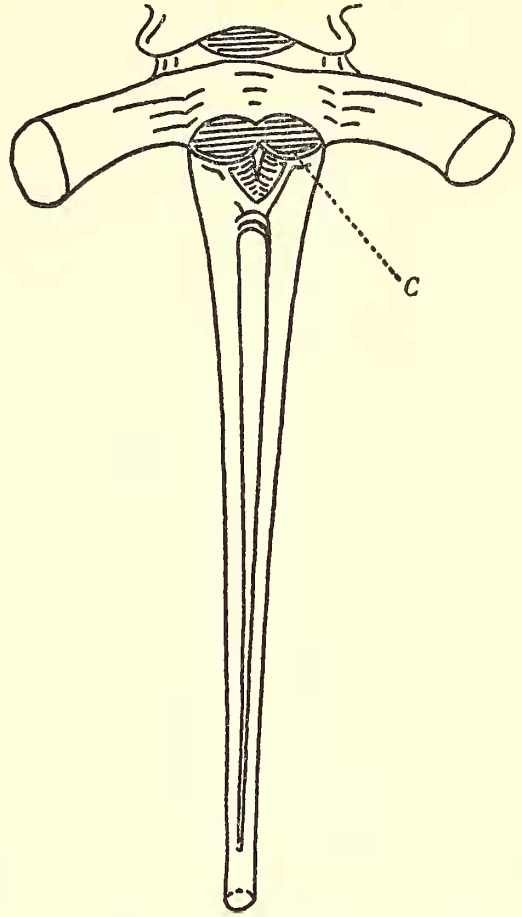
Our analysis leaves five frogs in this group. They may be distinguished by the following compiled key.

- 1a. Fingers without disks, toes webbed to middle of terminal dilation, prevomerine teeth between choanaeGenus *Pseudis*
- 2a. Adults 40 mm or more in standard length*P. paradoxus*
- 2b. Adults not exceeding 35 mm in standard length.
- 3a. Back and upper surfaces of limbs covered with spinous warts*P. meridionalis*
- 3b. Back and upper surfaces of limbs smooth*P. minutus*
- 1b. Disks on fingers, toes webbed to base of terminal dilation, prevomerine teeth behind choanaeGenus *Lysapsus*
- 4a. Back and upper surfaces of limbs covered with spinous warts*L. limellus*
- 4b. Back and upper surfaces of limbs smooth*L. laevis*

PHYLOGENETIC RELATIONSHIPS OF PSEUDIS AND LYSAPSUS

As indicated in the preceeding section, the frog genera *Pseudis* and *Lysapsus* are divergent in a variety of morphological characteristics. *Pseudis* is a strictly aquatic frog but *Lysapsus* spends most of its time out of the water on floating water plants. The differences between the two genera both in structure and habitat might seem to indicate that they are distantly related. However, in spite of these differences, *Pseudis* and *Lysapsus* appear to be closely allied for they share one feature which appears to be unique among living salientians. Both genera possess a well developed accessory phalanx in all fingers and toes. This structure, analogous to the intercalary cartilages of the Hyliidae, Phrynomeridae and Rhacophoridae, forces a reconsideration of the phylogenetic position of these frogs.

Disregarding the artificial anuran classifications utilized during the nineteenth century and restricting our inquiry to the era of the more natural system adopted through the work of Nicholls (1916) and Noble (1922), as modified for the firmistral section by Parker (1934) and for the procoelous groups by Davis (1936), we find that *Pseudis* (and *Lysapsus*) have consistently been referred to either of two families. Noble (1931, p. 499) placed these frogs in the Bufonidae (sensu lato) in association with *Telmatobius*, *Cycloramphus*, *Eleutherodactylus* and their allies in the subfamily Pseudinae. According to Davis (1936) this assemblage forms part of the family Leptodactylidae. Most authors



TEXT-FIG. 4. Dorsal view of the sacral vertebra and urostyle of *Pseudis paradoxus*. The letter C indicates one of the condyles.

have followed the Noble-Davis familial reference of the genus. However, Parker as early as 1931 (p. 494) pointed out the occurrence of an "intercalary bone" in *Pseudis* and suggested the inclusion of the genus in the family Hyliidae. In 1935, Parker (p. 511) again emphasized the importance of the "intercalary bone," again stating that *Pseudis* could not be a leptodactylid and he erected a new subfamily within the Hyliidae for it. Since Parker's time little attention has been given the familial position of this group and it has with equal frequency been referred either to the Leptodactylidae or to the Hyliidae.

We cannot agree with either Noble's, Davis's or Parker's family allocations, for the differences between *Pseudis* and *Lysapsus*, when compared with the Hyliidae, are very pronounced, and the accessory phalanx so completely differentiates them from the Leptodactylidae that a new family seems necessary for their reception. This family

PSEUDIDAE, New Family

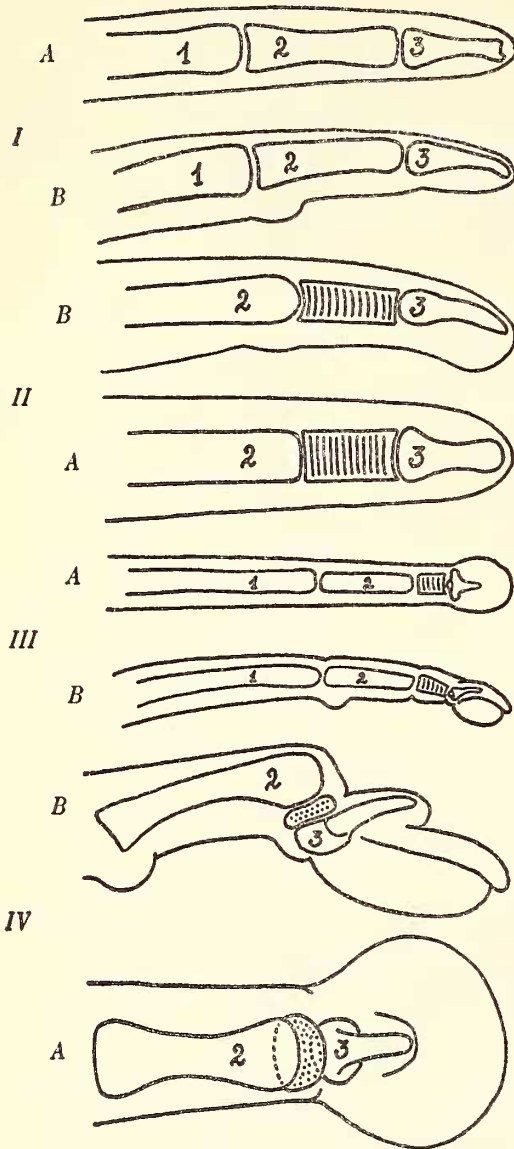
Pectoral girdle arciferal, omosternum present; maxillary, premaxillary and prevomerine teeth present; no Bidder's organ; a large accessory phalanx in each digit; sacral diapophyses cylindrical; skull completely roofed by bone; thumb opposable to fingers.

The new family is distinguished from the Hylidae by the presence of an accessory phalanx and cylindrical sacral diapophyses. The hylids have a small intercalary cartilage between the last two phalanges but as can be seen in Text-fig. 4 the relationships between the intercalary cartilage and the phalanges, and the position of the accessory phalanx, are entirely different in the two families. Further, the Hylidae usually have the sacral diapophyses dilated, but in a few species they are cylindrical.

In the nature of the sacral diapophyses, the Pseudidae show closest affinity with the Leptodactylidae. As the latter group is badly in need of revision and may be composed of several familial units, and as it is impossible to relate the Pseudidae with them except in a general way, we feel fully justified in segregating *Pseudis* and *Lysapsus* in a distinct family. Until the phylogeny of the "toothed" Procoela is clarified the Pseudidae are best described as leptodactylids with an increased phalangeal formula. There is ample precedent for giving groups with added phalangeal elements familial recognition, for the Hylidae are Leptodactylidae, the Phrynomeridae are Microhylidae and the Rhacophoridae are Ranidae in which intercalary cartilages have been developed. The accessory phalanges characteristic of the new family, while approximately similar in position to the cartilages in the several families of tree-frogs, are a different structure and appear to have been evolved for an entirely different function. In the arboreal groups the intercalary element helps in the efficient utilization of the digital disks as an aid to climbing. The accessory bone of the Pseudidae apparently arose as an extra element for the elongation and support of the fingers and toes as an aid to swimming. A similar modification has been noted in many aquatic mammals and the habits of the pseudid frogs fully confirm this hypothesis.

It should be mentioned that we have regarded the extra element in the digits of the Pseudidae as being the penultimate phalanx only through comparison with the condition in arboreal frogs. Actually, it is impossible to fix with certainty which of the phalanges is accessory without embryological study.

The evolutionary pattern within our new family seems rather simple. *Pseudis paradoxus* may



TEXT-FIG. 5. Diagrammatic representations of the toes in *Leptodactylus* (I), *Pseudis* (II), *Lysapsus* (III) and *Hyla* (IV). A. Dorsal aspect. B. Lateral view. Homologous phalanges are numbered the same in each type with the accessory phalanx of the Pseudidae and the intercalary cartilage of the Hylidae contrastingly marked. Note that the terminal phalanx of *Lysapsus* is not numbered because of its small size. This element corresponds with number 3 in the other frogs.

belongs to the suborder Procoela with which it agrees in having no ribs; presacral vertebrae eight in number, all procoelous; and coccyx free, with two condyles. The family may be described as follows.

be regarded as the primitive type because of the large extra phalanx, fully webbed toes, unmodified terminal phalanges, curved snout and the large size. In all these features, except the last, it appears to be fitted for an almost exclusively aquatic existence. The significance of the long finger and toe supports, complete toe webbing and the absence of terminal disks in such an aquatic frog is apparent, but the importance of the skull shape needs explanation. Among the neotropical aquatic frogs the general mode of position when floating is at an oblique angle to the water surface. *Pseudis* usually floats in a vertical position in the water with only the eyes and nostrils protruding. The curvature of the anterior portion of the skull provides for the emergence of the organs and makes possible almost complete submergence of head and body. The advantages of this modification to a strictly aquatic animal are obvious.

Pseudis minutus appears to have been directly derived from *paradoxus* or a *paradoxus*-like ancestor. It may represent another case of arrested development where the primitive form is a large species and its derivative, while similar in most characters, is of smaller size. The longer limbs credited to *minutus* as compared to *paradoxus* may indicate further specialization for aquatic life. *Pseudis meridionalis* appears to be closely related to, if not identical with, *minutus*. If valid, *meridionalis* may prove to be somewhat more advanced than *minutus*.

The genus *Lysapsus* seems to have arisen from *Pseudis*. It may have evolved directly from a large form similar to *paradoxus* or there may have been an intermediate stage similar in body size to *P. minutus*. The change from *Pseudis* to *Lysapsus* all appear to be along a line of increased specialization: the skull has flattened, the webbing of the toes is reduced, the additional phalanx has decreased in size and the terminal phalanges are highly modified to support a well-developed disk. In all these features *Lysapsus* has undergone changes to fit it for a less aquatic habitat. *Lysapsus* spends most of its time out of the water hopping about on the surface of floating or partially submerged plants. In its movements the highly modified digits are of value in providing traction on the slippery plant surfaces. Here, then, we see modification of the structures of a strictly aquatic frog into features parallel in general appearance and use to those of an arboreal group, such as the Hylidae. The opposable thumb, characteristic of the family and of use to *Pseudis* in grasping floating objects either as support or for food, and an aid in climbing in *Lysapsus*, is strikingly similar to the opposable thumb of some hylids. As can be seen

from this discussion we regard the similarities between the tree-frogs and *Lysapsus*, in the shape of the terminal phalanges, the disk and the opposable thumb, as well as the accessory phalanx, to be the result of a remarkable but not perfect parallelism in structure and habitat.

Within the genus, *L. limellus* seems most specialized, having shorter legs and spinate skin. *L. laevis* has slightly longer legs and a smooth skin, indicating a closer affinity to strictly aquatic *Pseudis*. More material is necessary to verify the validity of *laevis*.

ACKNOWLEDGEMENTS

We have been most fortunate to have at our disposal during the preparation of this discussion the advice and criticism of Dr. George S. Myers of Stanford University, one of the leading authorities on South American amphibiology. It was at his suggestion that description of a new family was undertaken and for this and many other favors we are greatly indebted.

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